

Attenuation of Photosynthetically Available Radiation (PAR) in Florida Bay: Potential for Light Limitation of Primary Producers

CHRISTOPHER R. KELBLE^{1,2,*}, PETER B. ORTNER², GARY L. HITCHCOCK¹, and JOSEPH N. BOYER³

¹ Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149

² Atlantic Oceanographic and Meteorological Laboratory, National Oceanic and Atmospheric Administration, 4301 Rickenbacker Causeway, Miami, Florida 33149

³ Southeast Environmental Research Center, Florida International University, Miami, Florida 33199

ABSTRACT: Light attenuation in marine ecosystems can limit primary production and determine the species composition and abundance of primary producers. In Florida Bay, the importance of understanding the present light environment has heightened as major upstream water management restoration projects have been proposed and some are already being implemented. We analyzed a 2-yr (2001–2003) data set of the light attenuation coefficient (K_t) and its principal components (water, chromophoric dissolved organic matter [CDOM], tripton, phytoplankton) obtained at 40 stations within Florida Bay, calibrated synoptic underway data to produce high spatial resolution maps, examined the potential for light limitation, and quantified the individual effect of each component upon light attenuation. Tripton was the dominant component controlling light attenuation throughout Florida Bay, whereas the contribution of chlorophyll *a* and CDOM to K_t was much smaller in all regions of Florida Bay. It was possible to accurately estimate the light attenuation coefficient from component concentrations, using either a mechanistic or a statistical model with root mean square errors of 0.252 or 0.193 m^{-1} , respectively. Compared to other estuaries, Florida Bay had the lowest overall K_t and the greatest relative contribution from tripton. Comparing the recent data to a study of Florida Bay's light environment conducted in 1993–1994, we found that overall water clarity in the Bay increased significantly, indicated by a nearly 3-fold decrease in K_t , as a result of lower tripton concentrations, although the percent contribution of each of the components to K_t is unchanged. Only the northwest corner of Florida Bay, an area comprised of approximately 8% of the Bay's total area, was found on average to have sufficient light attenuation to limit the growth of seagrasses. This is much less extensive than in 1993–1994, when seagrass growth was potentially limited by light at over 50% of the stations sampled.

Introduction

Light attenuation within the water column is of critical importance to both benthic and pelagic primary producers in marine ecosystems. The light available for primary production (photosynthetically available radiation [PAR]) is defined as the light reaching the depth of primary production at all the wavelengths of the visible spectrum. Attenuation of light in marine ecosystems is the result of inherent optical properties that include the absorption coefficient, scattering coefficient, and volume scattering function. The attenuation of PAR in marine ecosystems is expressed by the light attenuation coefficient, K_t , an apparent optical property, which can be calculated from a depth profile of PAR intensity. It has been shown in numerous studies that light attenuation can limit photosynthesis and the growth of primary producers (Cloern 1987; Duarte 1991; Kenworthy and Fonseca 1996). Traditionally, light limitation of pelagic phytoplankton growth is thought to occur when the euphotic depth, the depth at which light intensity is 1% of

the surface irradiance, is less than the mixing depth (Sverdrup et al. 1954). Seagrasses (higher plants) require considerably more light energy than unicellular phytoplankton, about 10–15% of the surface irradiance (Kenworthy and Fonseca 1996).

In most of Florida Bay, seagrass dominates overall system primary production because of the shallow depth (ca. 1 m on average) and suitability of sediments (Zieman et al. 1989; Fourqurean et al. 2001). Florida Bay underwent a massive seagrass die-off beginning in 1987 (Robblee et al. 1991) that attracted a great deal of attention, because of the Bay's importance as a nursery ground for many of the regional commercial and recreational fisheries including pink shrimp (*Farfantepenaeus duorarum*), spiny lobster (*Panulirus argus*), and numerous saltwater fish (Tilman 1989). Since the initial die-off, Florida Bay has been the subject of intense study and has been reported to have undergone additional ecological changes (Fourqurean and Robblee 1999; Hunt in press).

The exact cause of the seagrass die-off was never determined, although it is known that it was preceded by an extended period of higher than normal temperatures and salinities (Fourqurean

*Corresponding author: tele: 305/361-4330; fax: 305/361-4392; e-mail: Chris.Kelble@noaa.gov

and Robblee 1999). Among other components, the light available for photosynthesis can determine the rate at which seagrass beds recover from a die-off, and in some cases, which seagrass species will recolonize. A study of light attenuation in Florida Bay conducted after the die-off in 1993–1994 concluded that in a large area of Florida Bay seagrass growth might be inhibited due to light limitation (Phlips et al. 1995). That study was conducted during a large, persistent cyanobacterial bloom in north-central Florida Bay that was more intense and persisted longer than any observed in the ensuing decade (Boyer et al. 1999).

Ecological threats to the Everglades ecosystem (including Florida Bay) resulted in the passage of legislation by the United States Congress (WRDA 2000) and the State of Florida (EFA 1994; FFA 2000) to implement a Comprehensive Everglades Restoration Plan (CERP) with the goal of restoring the Everglades ecosystem to a sustainable condition. The 68 projects of CERP are intended to restore the quantity, timing, distribution, and quality of freshwater flow throughout the Everglades and delivery to adjacent marine ecosystems. This alteration of freshwater runoff to Florida Bay could influence water quality and primary production in the Bay. Increased freshwater deliveries may change the salinity distribution favoring (at least locally) particular seagrass or phytoplankton species. Particulates and dissolved organics introduced by the freshwater runoff may increase light attenuation, limiting the growth of primary producers.

Given the possible negative effects of increased light attenuation on diverse healthy seagrass beds, one of the ecological restoration targets or end points for Florida Bay, it will be necessary to monitor and assess light attenuation as restoration projects are implemented. Light attenuation in this system needs to be quantitatively understood in order to evaluate various restoration alternatives prior to construction. This information is a precondition for adaptive management of CERP with respect to Florida Bay.

Four major components contribute to light attenuation in the water column: seawater, phytoplankton, chromophoric dissolved organic matter (CDOM), and tripton (nonphytoplanktonic particulate matter). Several classification schemes have been proposed to define the light environment of aquatic ecosystems based on the dominant component(s) influencing light attenuation (Kirk 1980; Gordon and Morel 1983). Others have proposed a more quantitative approach determining the effect of each individual component upon light attenuation. The simplest of these quantitative partitioning approaches assumes that the effects of these 4 constituents are additive in nature (McPherson

and Miller 1987; Vant 1990). In this case, the light attenuation coefficient, K_t , is partitioned as follows:

$$K_t = K_{sw} + K_{CDOM} + K_{chl} + K_{tripton} \quad (1)$$

where K_{sw} is the partial attenuation coefficient for seawater, K_{CDOM} is the partial attenuation coefficient for CDOM, K_{chl} is the partial attenuation coefficient for chlorophyll *a* (chl *a*; a measure of phytoplankton abundance), and $K_{tripton}$ is the partial attenuation coefficient for tripton.

The applicability of this model to management issues (prediction of total attenuation under different scenarios and conditions) would be further enhanced if it were possible to quantitatively characterize each partial attenuation coefficient as a function of the specific attenuation coefficient, k^* , and concentration of that constituent. The simplest form of this application would be a simple linear relationship such as:

$$K_x = (k^*_x)(CONC_x) \quad (2)$$

where K_x is the partial attenuation coefficient for component *x*, k^*_x is its specific attenuation coefficient, and $CONC_x$ is the concentration. Such an approach would be particularly useful in water quality modeling, to the degree that it could enable a model to accurately estimate light attenuation from the concentrations of CDOM, chl *a*, and tripton. This approach enables various restoration alternatives to be evaluated in regard to the acceptable range and combination of the various components with respect to reaching and maintaining overall water clarity goals.

In this study, 2 yr of approximately monthly measurements at 40 fixed stations in Florida Bay are summarized with respect to light attenuation, tripton, chl *a*, and CDOM. These data are used in conjunction with hydrographic data to calibrate an underway water sampling system in order to obtain high spatial resolution maps of the individual components regulating light attenuation. Continuous high resolution data is essential because of Florida Bay's complex morphology and the high degree of isolation between basins (Fig. 1). The effect of each of the components on light attenuation is quantified and fit to models estimating K_t and the accuracy of these models is assessed. The high resolution K_t data is then superimposed upon a high resolution grid of the bathymetry of Florida Bay to determine if there are specific subregions of light limitation on primary producers.

Our prior inability to estimate K_t from component concentrations had been cited as a significant gap in the knowledge required for accurate modeling of Florida Bay water quality (Dortch et al. 1997).

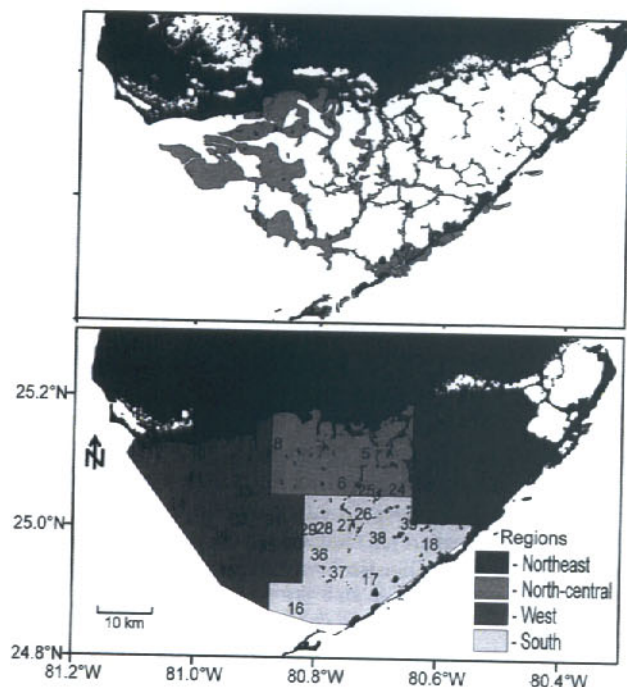


Fig. 1. A map of Florida Bay portraying the complex system of shallow mudbanks located within the Bay. The gray areas indicate the location of shallow (<1 m depth) mudbanks. A plot of the 40 discrete station locations in Florida Bay and the regional breakdown of Florida Bay into 4 distinct subregions as proposed by Nuttle et al. (2000).

As a result of this study, these relationships between the component concentrations and K_t can now be used by water quality modelers and restoration managers to predict what effects the implementation of CERP may have on light attenuation and in turn upon the primary producers of Florida Bay.

Methods

Data were collected using the R/V *Virginia K*, a 23-foot shallow water catamaran, operated by the National Oceanic and Atmospheric Administration's Atlantic Oceanographic and Meteorological Laboratory. Cruises were run at approximately monthly intervals from July 2001 until June 2003. Each cruise sampled 40 discrete stations along an underway sampling track (Fig. 1). The underway water sampling system consisted of a Seabird model 21 thermosalinograph, Japan Radio Corporation Global Position System receiver model DGPS 200, WetLabs C-Star transmissometer, Seapoint Chlorophyll *a* fluorometer, and a Seapoint CDOM fluorometer. The system was controlled by Seabird's SeaSoft software and recorded time, latitude, longitude, temperature, salinity, CDOM fluorescence (excitation $\lambda = 370$ nm; emission $\lambda = 440$ nm), chl *a* fluorescence (excitation $\lambda = 470$ nm; emission $\lambda = 685$ nm), and beam trans-

mission ($\lambda = 660$ nm) at 7-s intervals. The underway data was regressed against measured concentrations of chl *a*, CDOM, and tripton at the 40 discrete stations. These regressions were then applied to all the underway data to yield high resolution fields of estimated chl *a* biomass, CDOM concentration, and tripton concentration throughout Florida Bay.

Using a statistical model discussed in detail below, these estimated concentration fields were used to generate high resolution estimates of K_t in Florida Bay. These high resolution estimates were then standardized via the Surfer software program (Golden Software, Inc., Golden, Colorado) using the Kriging gridding process to produce estimates every hundredth of degree in latitude and longitude. This standardization allowed the data from the different cruises to be compared, in that it removed any variation between cruise tracks. It also allowed for the use of data from a high resolution survey of bathymetry in Florida Bay to estimate light limitation on primary production via the same standardization procedure.

At every discrete station, K_t was determined and samples were collected for chl *a* biomass and total suspended solids (TSS) concentration. CDOM measurements were made directly from the CDOM fluorometer calibrated to quinine sulfate units (QSU). Light penetration was measured using two 4π spherical quantum sensors, Li-Cor model LI-193 SA. The two sensors were placed 0.5 m apart on an L-shaped pole and measurements were taken every 0.25 m below the surface until the bottom was contacted or a depth of 2.5 meters was achieved with the bottom sensor. The light attenuation coefficient was then calculated from each set of light intensity measurements as follows:

$$K_t = \ln(E_{z1}/E_{z2}) / (z_2 - z_1) \quad (3)$$

where z_1 and z_2 are the depths of the light sensors and E_{z1} and E_{z2} are the light intensities at the two respective depths (Kirk 1994). Calculating K_t from concurrent light intensity measurements, removes errors introduced by collecting intensities in succession, caused for example by changes in cloud cover. Calculating numerous K_t values at varying depths for each station enables rigorous estimation of the mean and standard deviation of the light attenuation coefficient at each station for each survey.

Light limitation for phytoplankton was estimated from the light attenuation coefficient as the ratio of the euphotic depth, Z_{eu} , the depth at which light intensity is 1% of the surface irradiance, to the mixed layer depth, Z_m (in this study Z_m was assumed to be the same as the overall depth, because there is minimal stratification in Florida Bay and its average

depth is quite shallow). When this ratio is below 1.5, light attenuation is thought to play a minimal role in limiting phytoplankton growth; when the ratio is below 1.0, light attenuation plays a major role in limiting phytoplankton growth; and when the ratio is between 0.1–0.5, net production by phytoplankton drops below zero due to light limitation of photosynthesis (Cloern 1987). To calculate the euphotic depth, Z_{eu} , Eq. 3 was rearranged to yield the following equation:

$$Z_{eu} = 4.61/K_t \quad (4)$$

The ratio of the maximum seagrass colonization depth to the overall depth, Z , was used to determine the likelihood of light limitation upon seagrass growth. Where this ratio is consistently below 1.0 it is thought that seagrass growth is inhibited due to insufficient light reaching the benthos (Phlips et al. 1995). To generate first order estimates, and because this factor is both variable and was not measured in this study, the relative height of seagrass leaves above the bottom was not considered. Two different light intensities were used to estimate the maximum seagrass colonization depth. Maximum seagrass colonization depth, Z_{col} , was based on a review of worldwide data of seagrass maximum colonization depth along with corresponding light attenuation coefficients yielding the following relationship (Duarte 1991):

$$Z_{col} = 1.87/K_t \quad (5)$$

The second estimate is specific to turtle grass, *Thalassia testudinum*, which dominates the seagrass community over most of Florida Bay. It has been found that *T. testudinum* requires a minimum of 10% of the surface irradiance to reach the benthos (Zieman et al. 1999). Rearranging Eq. 3 to calculate the maximum seagrass colonization depth based on the depth of the 10% light level, Z_{loc} , yields the following equation:

$$Z_{loc} = 2.30/K_t \quad (6)$$

Chl *a* concentration was determined via a standardized filtration-extraction method using a 60:40 mixture of acetone and dimethyl sulfoxide (Shoaf and Lium 1976). The fluorescence of each sample was measured before and after acidification in order to correct for phaeophytin on a Turner Designs model TD-700 fluorometer. These fluorescence values were calibrated using known concentrations of chl *a* to yield chl *a* concentration in mg m^{-3} .

TSS concentration was determined gravimetrically at each station following Young et al. (1981). As large a volume of the sample as possible, with a minimum of 200 ml, was filtered onto preweighed

filters that were then dried and reweighed to calculate TSS via the following equation:

$$\text{TSS} = (W_{\text{post}} - W_{\text{pre}}) / V_{\text{filt}} \quad (7)$$

where W_{pre} is the prefiltration filter weight, W_{post} is the postfiltration filter weight, and V_{filt} is the volume filtered.

In order to calculate tripton the dry weight of the phytoplankton was subtracted from TSS. The dry weight of phytoplankton was determined based on the chl *a* biomass multiplied by the inverse of the percent of the dry weight of a phytoplankton cell that is chl *a*, equal to approximately 0.84% (Parsons 1961):

$$\text{Phytoplankton (dw)} = (\text{chl } a \times 119) / 1,000 \quad (8)$$

The percent weight of chl *a* per phytoplankton cell was assumed to be the mean of literature values corresponding to the families of phytoplankton found in Florida Bay, primarily cyanobacteria, diatom, and dinoflagellate (Parsons 1961; Phlips and Badylak 1996).

The CDOM fluorometer was calibrated to measure CDOM in QSU following Moore et al. (1993). This calibration is necessary to standardize fluorescence measurements from different instruments. The fluorescence signal voltage of standard concentrations of quinine sulfate was regressed against the concentration in QSU.

Results

DISCRETE STATION DATA

The results from the discrete station measurements were as follows. Measured light attenuation coefficients ranged from 0.13 to 2.82 m^{-1} , with the lowest value in the northeast Bay at station 40 in September 2002 and the highest value in the northwest Bay at station 10 in October 2001. The mean K_t values for each station ranged from 0.33 m^{-1} in the northeast (both stations 38 and 39) to 1.42 m^{-1} in the northwest (station 10). Chl *a* biomass had a minimum of 0.04 mg m^{-3} in the north-central region at station 4 in April 2002 and a maximum of 20.4 mg m^{-3} also in the north-central region at station 7 in July 2002. The mean chl *a* values varied from 0.26 mg m^{-3} at station 1 in the northeast to 4.03 mg m^{-3} at station 12 in the northwest. The CDOM values ranged from 3.67 QSU in the northeast at station 20 in July 2002 to 80.7 QSU in the north-central region at station 7 in September 2002. The mean CDOM varied between 10.4 QSU in the northeast at station 18 to 46.9 QSU in the north-central region at station 7. Tripton concentrations ranged from 0.01 g m^{-3} in the northeast and south at stations 26, 28, 29, 34, 37, and 40 to 47.0 g m^{-3} in the north-

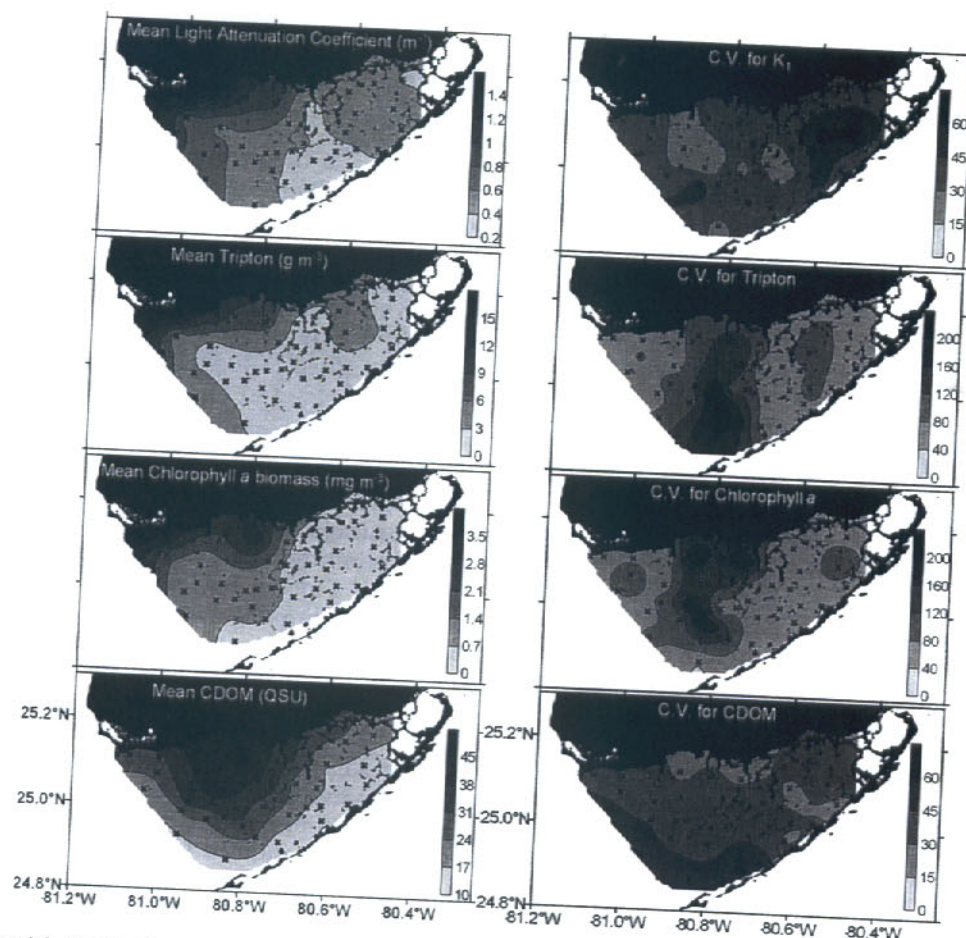


Fig. 2. The spatial distribution of the mean light attenuation coefficient (K_t ; m^{-1}), tripton (inanimate particulate matter) concentration ($g\ m^{-3}$), chlorophyll *a* biomass ($mg\ m^{-3}$), and chromophoric dissolved organic matter (CDOM) concentration (quinine sulfate units) in Florida Bay from July 2001 to June 2003. Spatial distribution of the coefficients of variation for K_t , tripton, chlorophyll *a*, and CDOM in Florida Bay from July 2001 to June 2003.

central region at station 7 in July 2002. The mean tripton concentrations varied from $1.39\ g\ m^{-3}$ in the north-central region at station 25 to $15.0\ g\ m^{-3}$ in the northwest at station 10.

Mean values of K_t , tripton, chl *a*, and CDOM over the 2-yr period of record are summarized in the contour maps of Fig. 2. The distribution of K_t and tripton are similar with peak values in northwest Florida Bay and the lowest values in the south-central Bay. Tripton and K_t also exhibit smaller secondary peaks in northeast Florida Bay corresponding to the area of the largest direct freshwater influence. Chl *a* has its maximum mean biomass in the northwestern Bay, as well, but it displays a secondary peak in the north-central Bay only slightly below the maximum biomass and has its lowest values in south and northeast Florida Bay. The CDOM distribution has a single maximum in the north-central Bay, close to shore, with values decreasing progressively with distance away from the peak concentration.

The coefficient of variation was used to estimate the variability at each station with respect to each of the four parameters. The spatial distribution of these coefficients of variation is depicted in Fig. 2. The coefficient of variation for K_t has a maximum in the northeast region, although the value of that coefficient is low. The relatively high variation in the northeast region was most likely a result of the direct localized runoff in this area that would alter the concentration of all three of the parameters that contribute to light attenuation (Nuttle et al. 2000). Tripton and chl *a* were the most variable parameters, with maximum coefficients of variation, in excess of 200, located in the center of the Bay for both variables. The variability of tripton in the central Bay most likely results from the physical isolation of this area due to shallow mudbanks that restrict exchange with adjacent areas to the northeast and the west (Fig. 1) in combination with seasonal wind mixing (Lawrence et al. 2004), also the seagrass die-off was most pronounced in this

region (Robblee et al. 1991) causing the sediments to destabilize. High variability in chl *a* is a product of seasonal cyanobacteria blooms in the north-central Bay that resulted in both the highest and lowest measurement of chl *a* biomass occurring in the north-central region (Phlips et al. 1999). The maximum coefficient of variation for CDOM along the western boundary is explained by seasonal discharge from Shark River that increases CDOM in this region (Clark et al. 2002).

ESTIMATES OF COMPONENT CONCENTRATIONS

To examine light attenuation and its component concentrations at spatial scales with higher resolution than that yielded by the discrete station data (presumably better reflecting the bathymetric complexity of the Bay), it is necessary to estimate the component contributions from the underway instrumentation. For CDOM this is straightforward by simply calibrating CDOM fluorescence to QSU. It is more complicated for chl *a* and TSS.

A multiple regression of the underway variables (chl *a* fluorescence, beam attenuation, temperature, salinity, CDOM) on measured chl *a* from the entire data set was statistically significant ($F_{4,705} = 158$, $p < 0.001$), yet unsatisfactory at estimating chl *a* biomass ($R^2 = 0.473$, root mean square error [RMS] = 1.32 mg m^{-3}), no doubt because the Bay has significant spatial and temporal differences in phytoplankton species composition and standing stock (Phlips and Badylak 1996). To account for these changes in phytoplankton community structure the ratio of chl *a* in situ fluorescence versus chl *a* extracted concentration (f:chl) was calculated. This ratio has been shown to differ significantly between different species of phytoplankton (McKee et al. 1999), and it was used here to divide the data into four nominal categories: cyanobacterial bloom (f:chl ≤ 0.11), diatom and cyanobacterial mixed bloom ($0.11 < \text{f:chl} \leq 0.25$), diatom bloom ($0.25 < \text{f:chl} \leq 0.55$), and no bloom (f:chl > 0.55). The calculation of four separate regressions on data sets sorted based on these categories provided a much improved estimation of chl *a* concentration from the underway data ($R^2 = 0.833$ to 0.925 , RMS = 0.422 mg m^{-3} , which is 39% of the mean and 2% of the maximum chl *a* biomass). To make estimates between discrete stations the weighted average ratios of the nearest stations were used.

The regression of the underway variables on TSS was also statistically significant, yet inadequate to reliably estimate TSS from the underway data ($F_{4,733} = 329$, $p < 0.001$, $R^2 = 0.642$, RMS = 3.63 g m^{-3}). The poor predictive power of this model is probably due to heterogeneity of the contributing sediments to TSS (Wanless and Tagett 1989), as well as seasonal differences in wind forcing events in

Florida Bay (Wang et al. 1994). A model similar to the one used for chl *a* was derived by dividing the data set into TSS types based on the ratio of beam transmission (from the transmissometer) to TSS concentration. This ratio has been shown by other researchers to vary with TSS type (McKee et al. 1999). The model of separate multiple regressions for each TSS type produced far superior results, with an RMS of 1.85 g m^{-3} or 44% of mean TSS and 3% of maximum TSS and coefficients of determination ranging from 0.666 to 0.902. The underway TSS estimations between stations used the weighted average ratios of the nearest stations to determine which equation to apply.

ESTIMATION OF K_t

To examine the contribution each of the four main components makes to K_t and to determine the utility of estimating K_t from the component concentrations two different approaches were taken. Both approaches are based on partitioning Eq. 1 into specific attenuation coefficients for each component (with the exception of seawater, which was taken to be a constant), yielding the following equation:

$$K_t = K_{sw} + (k^*_{CDOM} \text{CONC}_{CDOM}) + (k^*_{tripton} \text{CONC}_{tripton}) + (k^*_{chl} \text{CONC}_{chl}) \quad (9)$$

The first method is mechanistic in nature, whereby K_{sw} and the specific attenuation coefficients, k^* , for chl *a* and CDOM are based on experimental observations. $K_{tripton}$ is then calculated by subtraction of K_{sw} , K_{chl} , and K_{CDOM} from K_t and is regressed on tripton concentration in attempts to calculate $k^*_{tripton}$. The seawater constant, K_{sw} , was assumed to be 0.0384 m^{-1} (Lorenzen 1972). The k^* for chl *a* has been reported between 0.012 and $0.016 \text{ m}^2 \text{ mg}^{-1}$ by numerous researchers (Lorenzen 1972; Bannister 1974), and in a comparison of species specific k^*_{chl} among different families of phytoplankton, little variability was observed with a range of 0.012 to $0.015 \text{ m}^2 \text{ mg}^{-1}$ and a mean value of $0.014 \text{ m}^2 \text{ mg}^{-1}$ (Atlas and Bannister 1980). This mean value of $0.014 \text{ m}^2 \text{ mg}^{-1}$ was used for the mechanistic model.

Unfortunately, there are no relevant available values for k^*_{CDOM} . Previous light attenuation studies have estimated CDOM using dissolved organic carbon (Gallegos 2001), apparent color in platinum-cobalt units (McPherson and Miller 1987; Phlips et al. 1995), and absorption at 440 nm (g_{440} ; Vant 1990). None of these parameters is directly related to CDOM in QSU fluorescence units so none of the k^* s for these variables is applicable herein. It is well known that the type and number of chromophores, as well as the

chemical composition of CDOM, varies in different locations (Stedmon et al. 2000).

A regionally relevant k^*_{CDOM} was calculated based upon a series of measurements of CDOM (QSU) and absorption at $\lambda = 300$ nm from the Southwest Florida Shelf to the west Florida Bay transition zone (Clark et al. 2002). To extrapolate absorption by CDOM, a_{CDOM} , over the PAR spectrum the following equation from Hoge et al. (1993) was integrated from $\lambda = 400$ –700 nm:

$$a_{\text{CDOM}}(\lambda) = a_{\text{CDOM}}(\lambda_0) \exp[-S(\lambda - \lambda_0)] \quad (10)$$

where λ_0 is the reference wavelength (300 nm) and S is the spectral slope coefficient for CDOM. The spectral slope was calculated from a series of measurements of CDOM absorption spectra in Florida Bay by the Southeast Environmental Research Center (Boyer unpublished data). The measurements of PAR absorption by CDOM were divided by the corresponding CDOM concentration to calculate absorption per QSU. These values were then averaged, yielding a mean k^*_{CDOM} of $0.000424 \text{ m}^{-1} \text{ QSU}^{-1}$.

To calculate the k^*_{trip} it is first necessary to calculate K_{tripton} by subtracting the partial attenuation coefficients for seawater, chl a , and CDOM from overall K_t . The estimated K_{tripton} values can then be regressed on tripton concentration yielding the following equation:

$$K_{\text{tripton}} = 0.0492 \times \text{CONC}_{\text{tript}} + 0.296 \quad (11)$$

This regression is statistically significant ($F_{1,841} = 863$, $p < 0.001$) and relatively efficient ($R^2 = 0.506$, $\text{RMS} = 0.280$, which is 56% of the mean and 11% of the maximum K_{tripton}). The nonzero intercept is most likely the result of different sizes of suspended sediments in different areas of the Bay, as well as at different times of the year. It has been shown by previous studies that the sediments of Florida Bay are heterogeneous (Wanless and Tagett 1989); the same would be expected of the suspended sediments and, as a result, tripton. Not only are the wind patterns of Florida Bay known to be relatively variable but their effect upon wave generation (and mixing) is still more variable due to the complex bank topography (Wang et al. 1994; Lawrence et al. 2004). This heterogeneity in both time and space would affect both the type and size of tripton in Florida Bay and the k^*_{trip} , resulting in the appreciable intercept of Eq. 11.

Combining these estimates the equation for the mechanistic model is as follows:

$$K_t = 0.0384 + 0.014 \times \text{CONC}_{\text{chl}} + 0.000424 \times \text{CONC}_{\text{CDOM}} + (0.296 + 0.0492 \times \text{CONC}_{\text{tript}}) \quad (12)$$

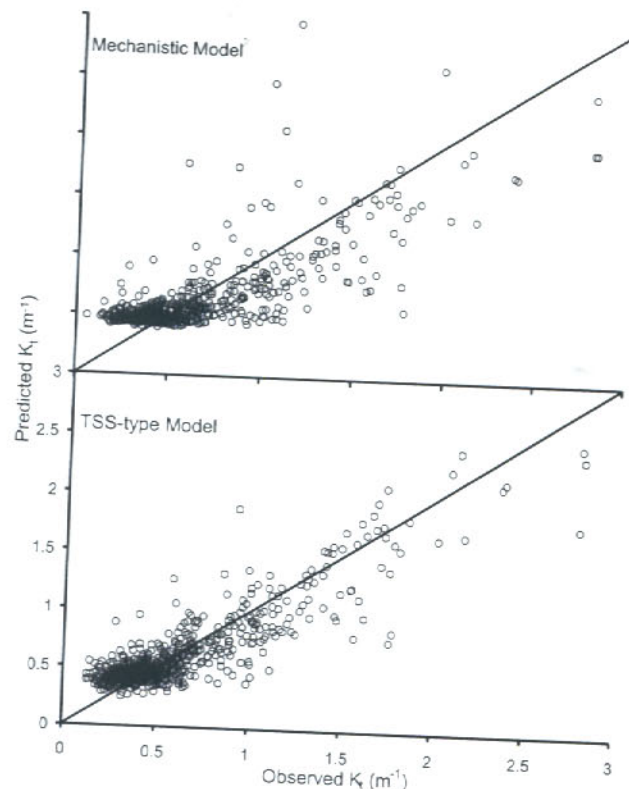


Fig. 3. Scatter-plot of predicted light attenuation coefficient, K_t , on observed K_t from the two different modeling strategies. The mechanistic model uses experimentally measured specific attenuation coefficients, k^* , to estimate K_t from the concentrations of tripton, CDOM, and chlorophyll a . The most efficient model uses four separate multiple linear regression models applied to the data after it was partitioned based on the ratio of beam attenuation to TSS. The gray line in each plot represents a perfect model.

Figure 3 shows the plot of predicted K_t from the mechanistic model (Eq. 12) versus observed K_t . The mechanistic model predicted K_t values from component concentrations with an RMS of 0.246 m^{-1} , which is 41% of the mean K_t value of 0.594 m^{-1} and 9% of the maximum K_t of 2.82 m^{-1} . This model efficiency is similar to that of a numerical water quality model already being used in another Florida estuary, Indian River (Christian and Sheng 2003). We conclude that it is reasonable to use the mechanistic model to estimate K_t in Florida Bay from component concentrations.

A second approach to modeling K_t uses multiple regression analysis of tripton, CDOM, and chl a concentration on K_t . While this approach lacks the physical constraints of the mechanistic model, it does (at least mathematically) take into account unmeasured influences that may covary with the three main components. The multiple linear regression model for the entire data set was statistically significant ($F_{3,649} = 375$, $p < 0.001$)

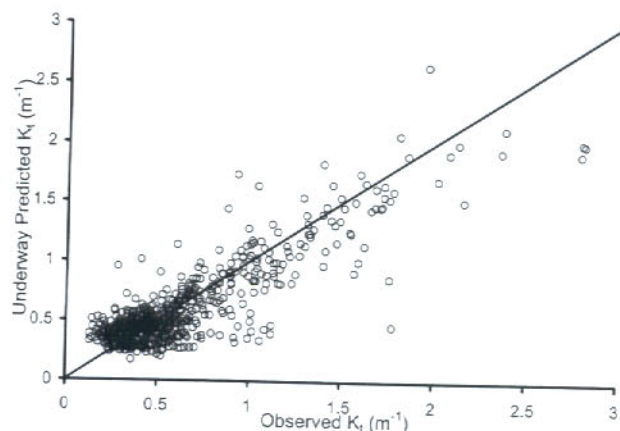


Fig. 4. Scatter-plot of the underway estimates of the light attenuation coefficient, K_t , versus the observed values. There is a minimal loss in accuracy when the underway estimates of component concentrations are used instead of the directly measured component concentrations.

and essentially similar in predictive efficiency to the mechanistic model ($\text{RMS} = 0.246 \text{ m}^{-1}$, $R^2 = 0.634$). A model analogous to the chl *a* model based on phytoplankton type and using the same three break points provides a still more accurate model with an RMS of 0.197 m^{-1} and $R^2 = 0.161$, 0.642 , 0.811 , and 0.819 . A multiple regression model estimating K_t using the TSS-type data set partitioning approach model proved to be the most accurate method (Fig. 3), with an RMS of 0.193 (32% of the mean K_t and 7% of maximum K_t) and coefficients of determination from 0.425 to 0.816 .

Because of its superior accuracy, the method of separate multiple regression models for each of the four different TSS-types was used to estimate K_t from the underway estimates of chl *a*, CDOM, and tripton (Fig. 4). The use of underway component concentration estimates instead of the actual measurements resulted in a minimal loss of model accuracy ($\text{RMS} = 0.206$, $R^2 = 0.338\text{--}0.830$).

Using the underway data yielded over 6,000 K_t estimates per survey, providing a high resolution image of K_t throughout Florida Bay. For each survey a grid was made that produced a K_t estimate every 0.01 degree of latitude and longitude. This was done to make the data sets between surveys comparable, since the survey track varies slightly between cruises. These high resolution grids of K_t were then averaged and contoured to produce the high resolution contour map of mean K_t from July 2001 to June 2003 shown in Fig. 5.

Unfortunately, none of the models were accurate at predicting K_t near the low end of the range of the data set, less than approximately 1.0 m^{-1} (Fig. 4). This is a significant weakness, because this low end

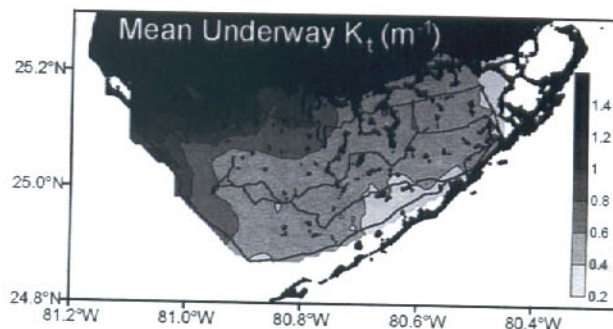


Fig. 5. Contour map of the mean light attenuation coefficient, K_t , from July 2001 to June 2003 as estimated from the underway data. The solid line depicts a typical survey track.

of the range is characteristic of much of Florida Bay on many occasions. On the other hand, the significance of this systematic deficiency is minimal with respect to estimating the effect of K_t on primary producers, because K_t must be relatively high in order to affect the growth of primary producers in Florida Bay. For example, a mean depth of 1 m is assumed for Florida Bay, K_t would have to be greater than 1.87 to negatively affect seagrass growth based on the most restrictive calculation.

Discussion

LIGHT LIMITATION OF PRIMARY PRODUCERS

To examine light limitation of pelagic phytoplankton, the underway K_t values were used to calculate the depth of the euphotic zone, Z_{eu} , according to Eq. 4. The mean Z_{eu} values were then compared to the mean water depth from a high resolution bathymetry study conducted in 1990 (Hansen and DeWitt 2000). Only in the extreme northwest corner of Florida Bay was the ratio of $Z_{eu}:Z_m$ less than 1.5 , indicating that light limitation may play some role in limiting phytoplankton growth. This area with a ratio less than 1.5 may be subject to some seasonal light limitation of phytoplankton, but even there it appears that light availability is not the dominant component controlling phytoplankton growth throughout the year. Nowhere in Florida Bay was the mean $Z_{eu}:Z_m$ ratio less than 1.0 during this 2-yr period.

To examine the potential for light limitation of seagrass growth, the maximum seagrass colonization depth was calculated from underway K_t according to Eqs. 5 and 6. The mean Z_{col} and Z_{loc} values were then divided by the water depth to calculate the ratios $Z_{col}:Z_m$ and $Z_{loc}:Z_m$. The resulting contour maps are shown in Fig. 6.

With either approach, there is a large area in the northwest corner of the Bay where the ratio is less than 1.0 , and seagrass growth would be expected to

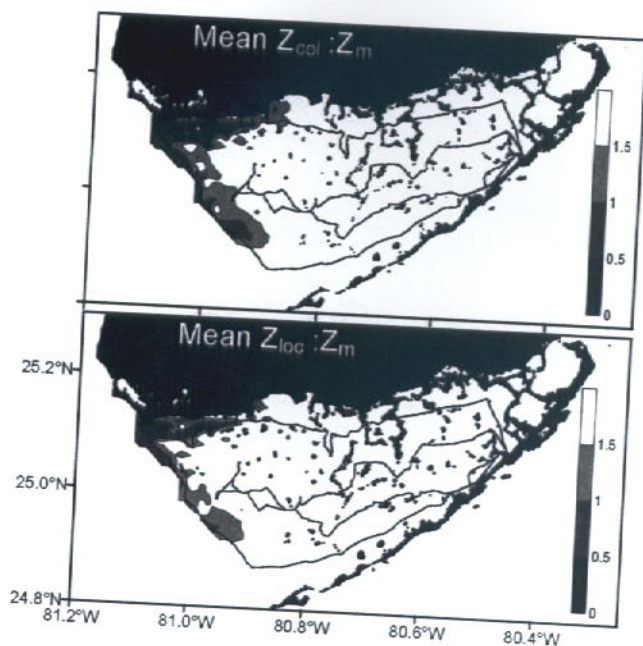


Fig. 6. Contour map of the ratio of the mean seagrass colonization depth to the water depth from July 2001 to June 2003. The top method is based on global data and the seagrass colonization depth is more restrictive, requiring just over 15% of the surface irradiance to reach the benthos, whereas the method specific for *Thalassia testudinum* requires only 10% of the surface irradiance to reach the bottom.

be inhibited due to insufficient light levels. It is estimated that seagrass growth could be inhibited in approximately 8% of Florida Bay due to light limitation. When ratios less than 1.5 are included to examine where light limitation may play some role, even if it is not the dominant component limiting seagrass growth, the area of Florida Bay affected nearly doubles to 14%, still centered in the northwestern corner of Florida Bay.

COMPONENT CONTRIBUTIONS TO K_t

To understand and predict the effects of individual components upon K_t , the mechanistic model is preferred. While its accuracy was less than the statistical model, the specific attenuation coefficients, k^* , for each variable are based on controlled experiments, whereas the pseudo- k^* s produced by linear regression include the effects of other components that covary with the component of interest. The experimentally based k^* s for chl *a* and seawater have been proven to be highly accurate in various studies (Lorenzen 1972; Atlas and Bannister 1980). The percent contribution of each component was calculated using the mechanistic model, by estimating K_t as well as the partial attenuation coefficients for seawater, chl *a*, CDOM, and tripton for each underway data point.

TABLE 1. Mean K_t (m^{-1}) for all of Florida Bay and each of the four subregions shown in Fig. 1. Mean percent contribution to K_t from seawater, chlorophyll *a*, tripton, CDOM, and unknown for the same areas. All data was calculated from the underway instrumentation.

	K_t (m^{-1})	K_{sw}	K_{chl}	$K_{tripton}$	K_{CDOM}
Average	0.588	8	2	89	1
North-central	0.633	7	3	88	2
Northeast	0.473	9	1	89	1
South	0.468	9	2	88	1
West	0.734	7	3	89	1

Mean underway K_t and the mean percent contribution by each of the four main components are shown in Table 1 for the entire Bay and for each of the four regions shown in Fig. 1. Florida Bay has been separated into distinct subregions because the isolation between basins, resulting from the mudbanks, has resulted in considerable heterogeneity with respect to nearly all ecological variables including, but not limited to seagrass (Zieman et al. 1989), sediments (Wanless and Tagett 1989), freshwater influence (Nuttall et al. 2000), fisheries (Tilman 1989), benthic mollusks (Turney and Perkins 1972), water quality (Boyer et al. 1997), and light attenuation (Phlips et al. 1995). The four subregions used in this study are similar to those used by Phlips et al. (1995) and Nuttall et al. (2000), and are based on physical factors: the geomorphology of the mudbanks (Fig. 1), freshwater inflow influence, and advective connections.

Differences between the four subregions of Florida Bay with respect to the contributions of various components to attenuation were remarkably small, although there was a considerable variation in mean K_t values that ranged between $0.468 m^{-1}$ in the south region to $0.734 m^{-1}$ in the west region. The relative contribution of each of the components to K_t (Table 2) was nearly identical in every region of Florida Bay. Tripton was the dominant contributor to light attenuation in all four subregions and accounted for 88% to 89% of K_t in every region. Tripton dominance is further evidence by the fact that the tripton distribution and K_t distribution (Fig. 2), are nearly indistinguishable. K_t increases with tripton and the tripton contribution to K_t is nearly constant over the four subregions. The contribution of seawater to K_t is the second most influential component to light attenuation, varying from 7% in the west and north-central to 9% in the south and northeast. Since the contribution of seawater to K_t is a constant, its percent contribution is an inverse function of the overall K_t distribution (Fig. 2). The contribution of chl *a* and CDOM to K_t in Florida Bay is negligible in all regions. The contribution of chl *a* to K_t varied from 3% in the west and north-central regions where chl

TABLE 2. The mean light attenuation coefficient, K_t , and the mean percent contribution of each component to K_t for 5 different light attenuation studies in Florida estuaries.

	K_t (m^{-1})	K_{tript}	K_{DOM}	K_{chl}	K_{nw}
Florida Bay (2001–2003)	0.3–1.4	89	1	2	8
Florida Bay—reported (Phlips et al. 1995)	0.8–2.8	75	7	14	4
Florida Bay—recalculated (Phlips et al. 1995)	0.8–2.8	85	7	4	4
Indian River Lagoon (Christian and Sheng 2003)	0.5–2.5	61	25	10	4
Charlotte Harbor (McPherson and Miller 1987)	0.5–6.0	72	21	4	3
Tampa Bay (McPherson and Miller 1994)	0.5–1.4	54	13	27	6

a biomass is at a maximum to 1% in the northeast where chl a concentration is lowest. The contribution of CDOM to K_t was even less, varying from 2% in the north-central region where CDOM values are highest to 1% in the other three regions. The small amount of variation in the light environment of Florida Bay is all the more remarkable, because so many other water quality and ecological parameters show large systematic differences between the subregions of the Bay (Boyer et al. 1997; Nuttle et al. 2000).

The percent contribution of each component to K_t , and the K_t value itself, are compared to three other Florida estuaries in Table 2. The overall light attenuation in Florida Bay was significantly less than that reported for other estuarine systems in Florida. Tripton dominated the light attenuation in all four estuaries, with Florida Bay receiving the greatest contribution at 89%, followed by Charlotte Harbor at 72%, Indian River at 61%, and Tampa Bay at 55%. With respect to the other components, the light environments of the four estuaries were significantly different. Florida Bay did not receive a significant contribution to K_t from either CDOM or chl a , whereas Charlotte Harbor and the Indian River Lagoon both had CDOM as the second leading contributor to K_t . Although Charlotte Harbor had no significant contribution from chl a , in Indian River chl a accounted for 10% of K_t . In Tampa Bay chl a was the second leading contributor to K_t at 27%, while CDOM accounted for 13% of light attenuation.

TABLE 3. Mean K_t , tripton, and chlorophyll a concentrations for all subregions of Florida Bay from this study and the prior study of light attenuation in Florida Bay (Phlips et al. 1995).

		K_t (m^{-1})	Tripton ($g\ m^{-3}$)	Chlorophyll a ($mg\ m^{-3}$)
Entire Bay	2001–2003	0.588	4.05	1.08
	1993–1994	1.47	16.0	5.04
North-central	2001–2003	0.633	3.82	1.33
	1993–1994	2.08	17	11.7
Northeast	2001–2003	0.473	2.74	0.384
	1993–1994	0.95	11.2	1.31
South	2001–2003	0.468	2.07	0.635
	1993–1994	0.97	11.3	3.14
West	2001–2003	0.734	6.74	1.81
	1993–1994	2.01	26.2	4.26

The lack of a significant relative contribution from chl a and CDOM to K_t in Florida Bay results from lower concentrations of these constituents, and not from having drastically higher tripton concentration, as indicated by Florida Bay having the lowest mean K_t of the four Florida estuaries. This is further evidenced by the fact that mean tripton concentration for this study ($4.05\ g\ m^{-3}$) was lower than Indian River ($7.83\ g\ m^{-3}$) and Charlotte Harbor ($10.0\ g\ m^{-3}$), the other two estuaries for which absolute tripton concentrations were reported.

These relatively lower component concentrations are a result of the physical regime in Florida Bay. The shallow mudbanks and secluded basins act to dampen physical forcing, limiting the extent of sediment resuspension despite the shallow water depth (Wang et al. 1994). This, in turn, decreases nutrient resuspension (Lawrence et al. 2004) and along with the separation between nitrogen and phosphorous sources (to the east and west, respectively; Boyer et al. 1997) helps keep the chl a biomass low. The relatively low amount of freshwater runoff into Florida Bay (Nuttle et al. 2000), and its containment due to the aforementioned isolation, results in significantly lower average CDOM values. It is the diminished concentration of tripton, CDOM, and chl a that results in lower light attenuation than that measured in other Florida estuarine systems. This might be an oversimplification, as it does not account for regional differences in phytoplankton species composition, CDOM chromophores, and perhaps most importantly for the fact that Florida Bay sediments are primarily composed of calcium carbonate and have a high reflectance (Wanless and Tagett 1989).

COMPARISON TO 1993–1994

The recent data are compared to the only previous systematic study of the light environment of Florida Bay (Phlips et al. 1995; Table 3). The most significant difference was that the chl a biomass was approximately 5-fold greater in 1993–1994. In the north-central region the difference was the largest, with about 10-fold higher chl a in 1993–1994. This high chl a biomass was primarily associated with a large, persistent cyanobacterial

bloom in 1993–1994 that was initiated and centered in the north-central Bay (Butler et al. 1995). While the other regions also showed elevated chl *a* biomass in 1993–1994, the differences were much less dramatic than in the north-central region.

There was also a difference in tripton concentration between the two studies, although the difference was less dramatic than it was for chl *a*. Tripton concentration was almost 4-fold greater in 1993–1994, and this difference was fairly evenly distributed throughout the Bay. It is purely speculative but not unreasonable that tripton concentrations were higher in 1993–1994 for two reasons. The 1993–1994 cyanobacterial bloom was resulting in various ecological changes including a die-off of sponges in the Bay (Butler et al. 1995). In shallow water environments like Florida Bay, filtration by benthic sponges can substantially affect overall water column particulate distributions. The 1993–1994 study was also conducted soon after the massive seagrass die-off of the late 1980s. Seagrass root structures stabilize sediments (Fonseca 1989), and such a die-off could cause the sediments throughout Florida Bay to be significantly less consolidated and more susceptible to resuspension events. On the other hand, the overall distribution of tripton was similar for the two studies and reflected not the distribution of seagrass die-off (Robblee et al. 1991) but the distribution of the forcing events, i.e., winds, waves and tides, that govern resuspension (Wang et al. 1994; Smith 1997). No comparison is possible between CDOM concentrations, because the prior study measured color in platinum-cobalt units that are not convertible to CDOM as measured herein.

Decreases in chl *a* and tripton concentration resulted in the substantial decrease in total light attenuation shown in Table 3. The north-central region had the largest difference in K_t values between the two studies, with mean K_t almost 4-fold higher in 1993–1994. The other regions all had K_t values approximately one half of those measured in 1993–1994. Despite this dramatic change in the overall light environment, the percent contribution of the various components to K_t in Florida Bay has not changed much from 1993–1994 to 2001–2003 as shown in Table 2. The percent contribution values from the first study had to be recalculated to permit direct comparison, because Phlips et al. (1995) used a k^* for chl *a* of $0.058 \text{ m}^2 \text{ mg}^{-1}$. Recalculating overall values with a k^*_{chl} of $0.014 \text{ m}^2 \text{ mg}^{-1}$ yielded relatively similar effects of each component upon PAR attenuation as in 2001–2003 (Table 2). The percent contribution of CDOM to K_t was higher in 1993–1994, but this may well be an artifact of the difference in measurement methods.

These differences in light attenuation imply substantial differences in the potential for light

limitation of primary producers. The potential for light attenuation to play a minor role in controlling phytoplankton growth in 2001–2003 manifested itself in only 1% of the Bay, whereas in 1993–1994 almost 12% of the stations displayed this potential. In 1993–1994, 6% of the stations showed the potential for light limitation to be the dominant component controlling phytoplankton growth, but nowhere in the Bay in 2001–2003 was light limitation observed to be the dominant component controlling phytoplankton growth.

The potential for light limitation on seagrasses was significantly more pronounced in 1993–1994 with 11 of the 17 stations having mean $Z_{\text{col}}:Z_m$ ratios less than 1.0 and all station's mean $Z_{\text{col}}:Z_m$ ratio was less than 1.5 (Phlips et al. 1995). In 2001–2003, only 8% of the Bay had a $Z_{\text{col}}:Z_m$ ratio less than one and 14% less than 1.5. If the period 2001–2003 is representative, since 1993–1994 the water clarity in Florida Bay has improved dramatically, reducing the risk of light limitation inhibiting seagrass growth in Florida Bay. Some areas in the northwest Bay may still be at risk, but this is a small portion of the Bay compared to 1993–1994 when the entire Bay was at risk.

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